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Behavioral plasticity of modern and Cenozoic burrowing thalassinidean shrimp

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Abstract

The use of trace fossils as paleoenvironmental indicators is based on empirically-derived and tested links between environmental conditions, behavior, and trace fossil morphology. Four approaches were used to assess how faithfully and at what resolution trace fossils, as mirrors of behavior, reflect environmental change: (1) comparing the abundance and morphology of *Ophiomorpha nodosa* in tidal channel-margin and tidal channel-axis facies (Miocene, Delaware); (2) determining the range of morphology of *O. nodosa* produced under unchanging environmental conditions (within the channel-margin facies); (3) evaluating the behavioral response of the modern burrowing thalassinidean, *Neotrypaea californiensis*, in Mugu Lagoon, California to an environmental perturbation, namely the burial of layers of glass plates; and (4) assessing how ancient producers of *Ophiomorpha* dealt with obstacles presented by dense shell and coral accumulations (Miocene, Maryland; Pleistocene, Bahamas). Comparison of *Ophiomorpha nodosa* in channel-margin versus channel-axis facies indicated that *O. nodosa* was significantly more abundant in the channel-margin facies. However, there was no significant difference in burrow characteristics (exterior or interior diameter, wall thickness) between the facies. As recorded by *O. nodosa*, its thalassinidean producer did not modify its behavior in response to conditions in the tidal channel axis. Rather, the tracemakers tended to avoid the channel axis, as indicated by the reduced abundance of *O. nodosa*. In contrast, *O. nodosa* within the channel-margin facies was highly variable in degree of pelletization of the burrow wall, in burrow fill and definition of the burrow margin, and in architecture of the burrow system. Variation in *O. nodosa* found within the channel-margin facies reflected behavioral flexibility in the absence of environmental change. Modern burrowing shrimp adapt to barriers (layers of glass plates) implanted within the substrate. They alter the geometry and depth of their burrow systems; they may even share shafts that penetrate the barrier. Meters thick Miocene shell beds (Maryland) in which the shells are not densely packed contain *Ophiomorpha* and *Thalassinoides*; the producing thalassinideans were able to penetrate and move through the shell bed. Similarly, Pleistocene thalassinideans maneuvered around coral rubble in Bahamian fossil coral reefs. However, Miocene decimeter-thick shell beds that are densely packed and well sorted are not penetrated by thalassinidean burrows, implying that thalassinidean behavioral flexibility was not sufficient to penetrate densely packed shell beds. Likewise, in the Bahamian reefal settings, *Ophiomorpha* producers formed extensive maze systems immediately above impenetrable lithified surfaces in the reefal sequence. Behavior of thalassinidean shrimp is neither tightly constrained nor highly programmed, and there is no indication that this has changed since Miocene time. Small changes in morphology of traces produced by thalassinideans cannot be used to identify subtle changes in environmental conditions. Shrimp vary

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behavior apparently “whimsically”, as well as in response to environmental change. If this is true of animals other than thalassinideans, the challenge to the ichnologist is to distinguish between “background” and “environmentally triggered” behavioral variation as recorded in the trace fossil record. © 2001 Elsevier Science Ltd All rights reserved.

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1. Introduction

The use of trace fossils for answering sedimentologic and/or paleobiologic questions is predicated upon linkages between environmental conditions, animal behavior, and morphology of the traces produced by the animals. For any set of environmental parameters, there also are certain optimal animal behaviors. Changes in environmental conditions cause changes in animal behavior that are reflected in shifts in various attributes of the traces produced. The application of these principles suggests that variation in trace fossils reflects environmental changes and implies that the type of environmental change can be inferred from careful evaluation of the morphological change in the traces.

The validity of these principles has been upheld by empirical testing. However, in spite of their usefulness, particularly in elucidating depositional conditions (e.g. Seilacher, 1967; Crimes and Harper, 1970, 1977; Frey, 1975; Ekdale et al., 1984; Curran, 1985; Maples and West, 1992; Bromley, 1996), important questions about the causal relationships between environmental, behavioral, and (trace) morphological change remain unanswered. These questions include, but are not limited to: (1) How much behavioral and morphological variation occurs in the absence of change in environmental conditions? With only minimal change, what is the range in behavior within individual tracemaker species, and how is this recorded in trace morphology?; (2) What triggers behavioral change in modern animals? Do animals respond to changes in food supply or sediment consistency by altering their behavior — alterations that would be reflected in trace morphology?; (3) Are there criteria for distinguishing between “background variation” in behavior and trace morphology and behavior/trace-morphological change caused by environmental parameter changes?

This paper reports on attempts to answer some of these questions (Table 1). We focus on the modern

thalassinidean shrimp *Neotrypaea californiensis* (formerly *Callianassa californiensis*) in Mugu Lagoon, California, and the thalassinidean-produced trace fossil *Ophiomorpha nodosa* from Miocene deposits of the US Atlantic Coastal Plain and late Pleistocene reefal deposits in the Bahamas. First, characteristics of Miocene *Ophiomorpha nodosa* formed under slightly different estuarine environmental conditions — channel margin versus channel axis — are compared. Second, the amount of variation in *O. nodosa* from within these channel-margin deposits is assessed. Third, the behavioral response (and change in trace morphology) of modern *Neotrypaea californiensis* to environmental disturbance is documented. The perturbation consists of burying a layer of artificial shells, thus simulating the natural occurrence of shell concentrations in sediment inhabited by these infaunal, deep-tier thalassinideans. Finally, the ability of the Miocene and Pleistocene callianassid producers of *O. nodosa* to deal with environmental (substrate) disruption caused by accumulations of shells and coral rubble is documented.

2. Comparison of *Ophiomorpha nodosa* produced under different paleoenvironmental conditions

2.1. Geological setting

Ophiomorpha nodosa occurred in both tidal channel-axis and tidal channel-margin deposits of a 5 m thick section of the Miocene Calvert Formation that was temporarily exposed near Smyrna, Delaware, in 1994 during excavation related to a wetlands remediation project (Fig. 1; Benson, 1998; Miller et al., 1998; Ramsey, 1998). *O. nodosa* is common in facies of similar age and character on the US Atlantic and Gulf coastal plains and elsewhere (e.g. Patel and Shringarpure, 1990; de Gibert et al., 1998). Both the channel-axis and channel-margin deposits consisted of fine- to medium-grained sand. Sets of large-scale

Table 1
 Questions asked in this study and information about study areas used to answer these questions

Questions asked	Study area	Age	Formation	Lithology	Depositional environment	References
1. How does <i>Ophiomorpha nodosa</i> formed in two environments differ?	Pollack Farm Site, Smyrna, Delaware (US Atlantic Coastal Plain)	Miocene	Calvert Fm	Variable quartz sands and mud; compacted but not lithified	Estuarine: Channel axis, Channel margin	Benson, 1998; Ramsey, 1998; Miller et al., 1998
2. How does <i>Ophiomorpha nodosa</i> vary in absence of environmental change?	As above	As above	As above	Largely quartz sands	Estuarine: Channel margin	As above
3. How does the modern thalassimid <i>Neotrypaea californiensis</i> respond to environmental perturbations?	Mugu Lagoon, California	Modern	n/a	Largely quartz sands	Behind barrier; along margin of tidal channel	Warne, 1971; Miller, 1984
4. How did Miocene and Pleistocene producers of <i>Ophiomorpha nodosa</i> respond to shell and coral rubble accumulations?	Calvert Cliffs, Chesapeake Bay, Maryland, USA	Miocene	Choptank and St. Mary's Fms	Variable quartz sands to mud; poorly to unlithified	Shallow marine	Kidwell, 1989
	Great Inagua and San Salvador, Bahamas	Pleistocene		Shelly calcarenites (lithified carbonate sands with coral reef rubble)	Shallow marine — reefal	Curran and White, 1991; Curran, 1994; Wilson et al., 1998

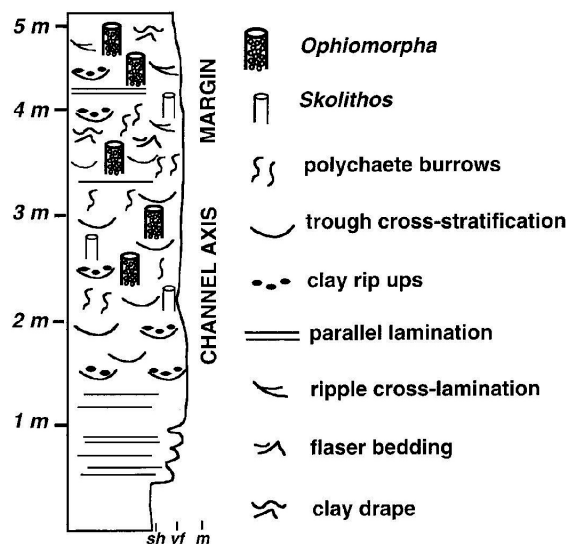


Fig. 1. Stratigraphic section of the Calvert Formation (Lower Miocene) formerly exposed at a wetlands remediation site, Smyrna, Delaware. Sequence recorded tidal channel deposition (Ramsey, 1998; Miller et al., 1998); both channel-margin and channel-axis deposits were present.

trough cross-stratification 10–20 cm thick and 1.00–1.25 m wide dominated the channel axis facies, and troughs commonly were lined with clay rip-up clasts. In contrast, the predominant bedding in the channel-margin facies was ripple cross-lamination and flaser bedding; clay drapes were common (Miller et al., 1998). Features of the channel-margin facies (ripple cross-stratification, abundance of clay drapes) reflect lower flow regime conditions than those of the channel-axis facies (large scale trough cross-stratification, concentrations of clay rip-up clasts, absence of clay drapes) that indicate higher flow regime conditions.

2.2. Trace fossil abundance

Cursory comparison of the number of *Ophiomorpha nodosa* in the channel margin versus channel-axis facies suggested that specimens of *O. nodosa* were more abundant in the channel-margin deposits. This observation was tested by counting the number of burrows in eleven 1 m² grids on vertical exposures of both the channel margin and channel-axis deposits. (A burrow was defined as an isolated segment of *O. nodosa*.) Mean burrow density in the channel margin was 16.5 versus 0.36 m⁻² in the channel-axis deposits.

This difference was statistically significant (A *F*-test showed variances to be inhomogeneous so a Student's *t*-test modified for inhomogeneity of variances was used: $t = 5.81$; $df = 11$; $p < 0.05$; Dixon and Massey, 1969).

2.3. Morphological variation

The morphological characteristics of *Ophiomorpha nodosa* best revealed by the Miocene channel deposits at the Smyrna, Delaware site were interior and exterior burrow diameter and burrow-wall thickness. Characteristics of the *Ophiomorpha* burrow wall are known to change with changes in substrate and flow conditions (Frey et al., 1978; Bromley, 1996). We predicted that: (1) burrow walls would be thicker in the (higher energy) channel axis deposits; and (2) burrow diameters would be larger in the channel margin facies, as a result of marginalization of juveniles to other, less desirable habitats or slower growth because of resource scarcity. One of us (Miller) observed in Mugu Lagoon, California, restriction of juveniles of *Neotrypaea californiensis* (less than 1.5 cm in length) to the uppermost subtidal zone of a tidal channel that contained few adults. This zone was lower than the lower intertidal zone heavily populated by adult *N. californiensis* (169 m⁻²; Miller, 1977). We assessed differences in size and thickness of the burrow walls between *O. nodosa* in the channel-margin and channel-axis facies. Neither of these predictions was substantiated. There was no significant difference in specimens of *O. nodosa* in channel-axis (CA) versus channel-margin (CM) environments when the following characteristics are compared: mean exterior diameter (CA, mean = 2.92 cm; $n = 14$; CM, mean = 2.40 cm; $n = 126$; $t = 0.162$; $df = 100$; $p < 0.01$); mean interior diameter (CA, mean = 1.49 cm; $n = 7$; CM, mean = 1.68 cm; $n = 97$; $t = 0.913$; $df = 100$; $p < 0.01$) or burrow thickness (CA, mean = 0.63 cm; $n = 7$; CM, mean = 0.76 cm; $n = 97$; $t = 0.162$; $df = 100$; $p < 0.01$; Dixon and Massey, 1969).

2.4. Interpretation

The producer of *Ophiomorpha nodosa* preferred inhabiting sands at the margins of the tidal or estuarine channel rather than those in the axis of the channel. Similarly, the modern *Neotrypaea californiensis* was

more abundant along margins of tidal channels in Mugu Lagoon, California, than in the center of the channel (Miller and Myrick, 1992). During high tidal flow in the channel, some sand carried in the bed load fell into open burrow shafts (Miller, personal observation). The shrimp largely expel this sand from their burrows, but this is energetically expensive. As the cost of maintaining a burrow toward the center of the channel rises with increased avalanching of sand into the burrow, the number of burrow openings, a proxy for number of shrimp, decreases. This interpretation for the producer of *O. nodosa* throughout the Cenozoic is supported by observed greater abundance of *O. nodosa* in sandy facies deposited under lower energy conditions than very high energy conditions (Carter, 1978; Pollard et al., 1993).

The small number of *Ophiomorpha nodosa* specimens in the channel-axis precluded comparison of the architecture of the burrow systems in channel-axis and channel-margin deposits. Based on previous work, one would predict more shafts in the higher energy channel-axis deposits, and more three-dimensional boxworks and mazes in the channel-margin deposits (Frey et al., 1978; Anderson and Droser, 1998). However, in this example from the Miocene strata of Delaware, instead of changing behavior in the channel axis, as would be reflected by an approximately equal number (~97) of *O. nodosa* as in the channel-margin deposits, but predominantly shafts versus tunnels, the *Ophiomorpha* producers responded to the higher energy environment by avoiding it, resulting in very few specimens ($n = 14$) in the channel-axis deposits.

Likewise, there was no observed change in morphology of the burrow wall for Delaware Miocene traces in sands deposited in the channel margin versus those deposited in the channel axis. The burrow wall was not thicker in sands deposited under higher energy conditions, implying that the behavior controlling the thickness of the burrow wall did not alter with change in energy conditions. Similarly, the lack of difference in the burrow diameters (internal or external) in specimens of the channel-margin sands versus the channel-axis sands indicated that there was no significant difference in size between the two populations of callianassids. This suggests that the producers of *Ophiomorpha nodosa* did not relegate juveniles to less preferred habitats. It also implies that food and other resources

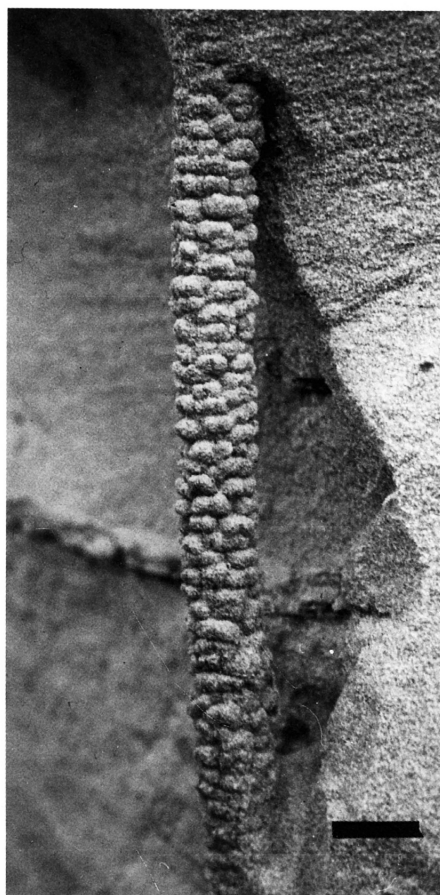


Fig. 2. Specimen of *Ophiomorpha nodosa* preserved in full relief. Note brick-like arrangement of pellets at top of shaft. Pellet arrangement becomes less regular downward. Miocene of Delaware; scale bar = 2 cm.

required for growth were available equally in both the channel-axis and channel-margin habitats. In sum, comparison of *O. nodosa* in deposits from the center versus margins of this Miocene tidal channel yielded no clear linkages between environmental differences and changes in optimal behavior and trace morphology.

3. Variation in *Ophiomorpha nodosa* in the absence of environmental change

3.1. Description of variation

To determine how much behavioral variation

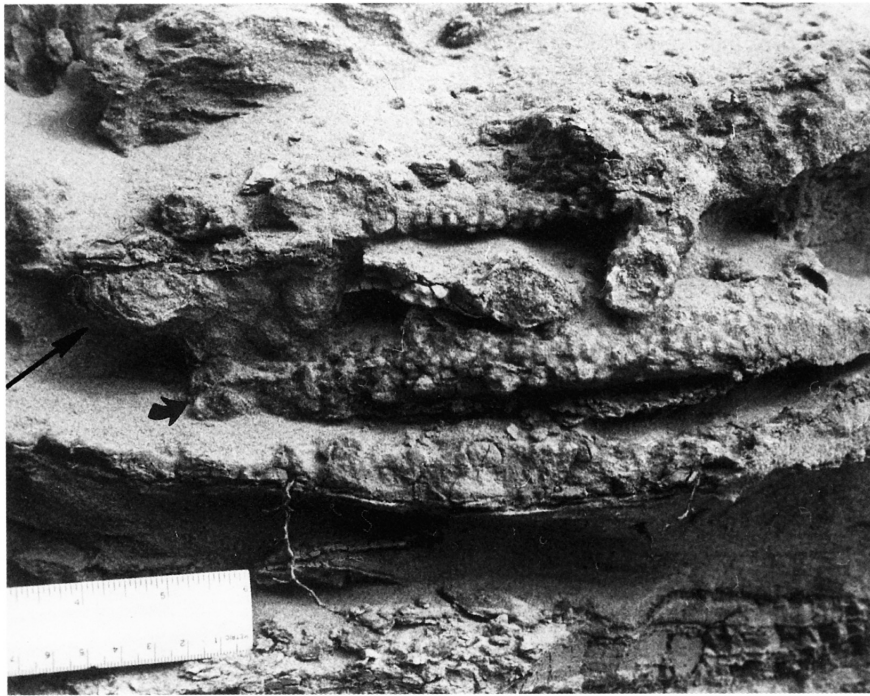


Fig. 3. Variable pelleting within *Ophiomorpha nodosa*. Tunnels in center of photo are well pelleted, whereas tunnel indicated by straight arrow lacks pelleting. Note close stacking of tunnels, two of which merge laterally into an unpelleted, vertically-oriented disorganized zone or poorly defined shaft with reworked fill. Curved arrow points to lower left margin of this zone. Some or all of the burrow components visible here probably belonged to the same three-dimensional burrow system (e.g. same specimen of *O. nodosa*). Miocene of Delaware; ruler is 2.5 cm wide.

occurs in the absence of environmental change, we assessed morphological variation in *Ophiomorpha nodosa* within the channel-margin environment of the Miocene sandbody (Table 1; Fig. 1). Characteristics evaluated include: (1) arrangement and packing of pellets; (2) distinctiveness of the burrow wall or margin and burrow fill; and (3) architecture of the burrow system.

The arrangement and packing of pellets in *Ophiomorpha nodosa* in the channel-margin deposits is highly variable. In some specimens, pellets are nearly brick-like in their uniformity and arrangement (Fig. 2). In others, the pellets are less carefully arranged or patchily distributed; some segments of tunnels lack pellets altogether (Fig. 3).

Whereas *Ophiomorpha nodosa* typically consists of pelleted tunnels and shafts that are either empty or passively filled (Frey et al., 1978; Fig. 4), the clarity and definition of burrow walls and nature of burrow

fill vary widely in *O. nodosa* from the Miocene tidal-channel margin deposits. Here well-pelleted, discretely-lined segments merge into zones of disrupted sediment with scattered pellets (Fig. 5). Other burrows, including some connected to disrupted zones (Fig. 6), have meniscate filling indicating either active rather than passive fill, or reburrowing.

The arrangement of tunnels and shafts of the burrow systems in the channel-margin deposits also was variable and not readily described as comprising either boxworks or mazes in the sense of Frey et al. (1978) (Fig. 4). As counted on the vertical exposure of the channel-margin deposits, tunnels outnumbered shafts by a ratio of 3:1. Many of the tunnels appeared to be isolated tubes. In rare cases, specimens branched, creating an overall inverted "Y" form (Miller et al., 1998). In other specimens, stacked tunnels (perhaps part of mazes) merged into central unlined vertical zones of

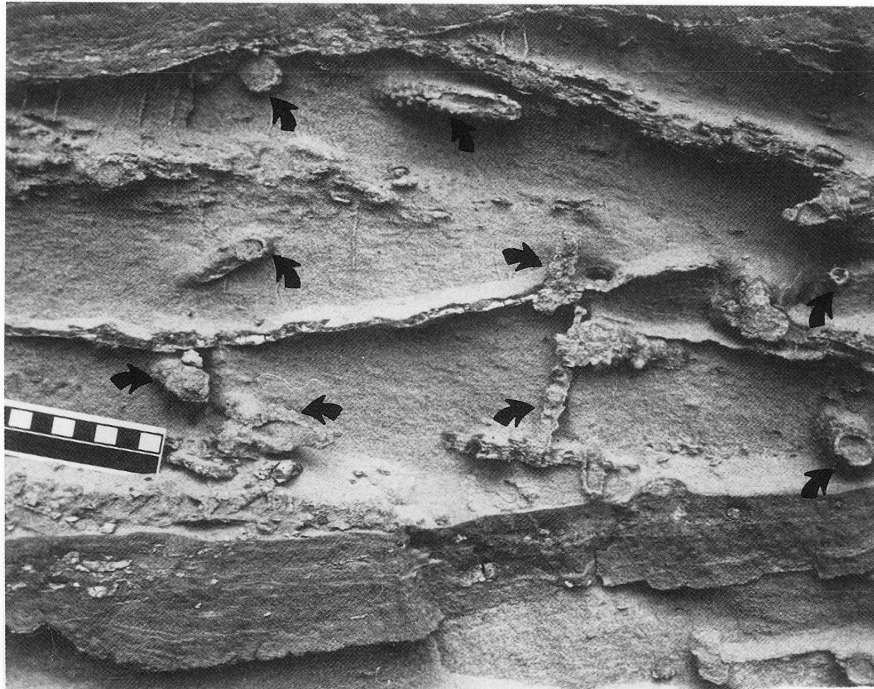


Fig. 4. Empty and passively filled shafts and tunnels of *Ophiomorpha nodosa*; some (not all) are indicated by arrows. Widely spaced tunnels and shafts are not organized into identifiable boxworks or mazes. Miocene of Delaware; scale has centimeter divisions.

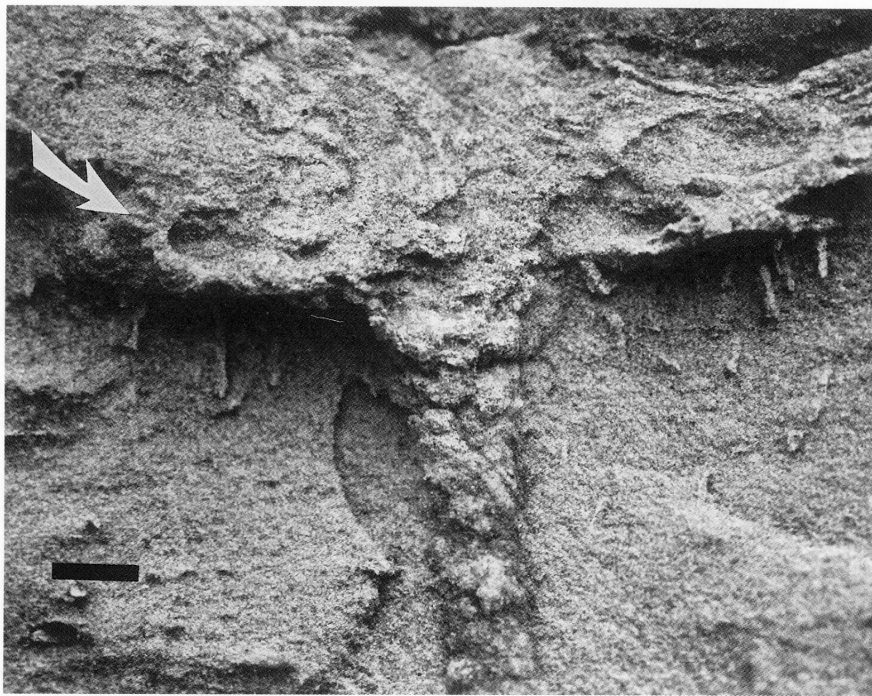


Fig. 5. Discrete, pelleted shaft changing upward into a tunnel (white arrow points to pelleted margin) and disorganized zone with swirled sediment and scattered pellets. Miocene of Delaware; scale bar = 1.5 cm.



Fig. 6. Pelleted shaft of *Ophiomorpha nodosa* exhibiting meniscate fill with pellets and suggesting reoccupation of the burrow after its initial construction. Shaft merges both upward and downward into disorganized zones with scattered pellets. Miocene of Delaware; scale bar = 1 cm.

disrupted sediment or shafts merged into horizontal zones of disrupted sediment (Fig. 3). Although we could not identify a shared three-dimensional architecture, it was clear that branching, interpenetration, and horizontal extension from vertical elements, as well as merging of disrupted zones with isolated, well-lined and pelleted tunnels and shafts were all common in occurrence.

3.2. Discussion

Ophiomorpha nodosa within the estuarine channel-margin deposits varied both in characteristics of the burrow wall and in architecture of the burrow system

(Table 2). In the Delaware channel-margin deposits, the variation occurred within a sand body deposited under a single set of environmental conditions, so variations in burrow wall and overall architecture cannot be interpreted as responses to changing environmental conditions. The changes from pelleted burrows to “disorganized zones” imply that the producer left the confines of the burrow to move freely within the substrate. Because the thickness and definition of burrow walls change markedly within individual burrow systems, we interpret the variations as resulting from behavioral plasticity intrinsic to the tracemaking organism. The only other possibility is that such variations are caused by environmental

Table 2

Variations in *Ophiomorpha nodosa* observed in this study, with behavioral and environmental interpretations. Overall, there is little observed difference other than in abundance between facies (environments), and considerable variation within a single facies (environment)

Within or between environments	Observation	Behavioral or environmental interpretation
Between: Comparison of <i>O. nodosa</i> in channel-axis and channel-margin facies	No significant variation in <i>O. nodosa</i> tunnel diameter or wall thickness between facies. <i>O. nodosa</i> more abundant in channel margin facies. Abundance too low in channel axis facies to compare architecture of burrow systems	Tracemakers did not respond to differences in environmental conditions by change in behavior. Did respond by avoiding higher energy channel-axis environment
Within channel-margin facies	Density and arrangement of pellets is highly variable	Behavior controlling pellet construction and arrangement is variable, not highly programmed
Within channel-margin facies	Burrows grade from open tunnels/shafts with well-defined walls to burrows with meniscate fill and low density of pellets, to poorly defined disorganized zones with scattered pellets	Burrow construction ranges from meticulous to haphazard. Producers move outside of in addition to within burrows. Burrows are re-occupied and modified
Within channel-margin facies	Tunnels outnumber shafts 3:1. Isolated shafts and tunnels are most common; closely stacked tunnels and associated shafts and disorganized zones are also common	Boxworks and mazes (Frey et al., 1978) are not recognizable. Burrow architecture highly variable in style within this facies

changes not decipherable from the stratigraphic record.

In contrast, previous workers have attributed variations in burrow morphology to behavioral responses to changing environmental conditions. Published observed morphological variants, in both burrow morphology and burrow-system architecture, and their interpretations are summarized in Table 3. None of the previously described morphological variations of *Ophiomorpha nodosa* (Table 3) were encountered in this study. Morphological variations that were observed (Table 2) occurred within the channel-margin deposits that do not record significant environment change.

Previous studies have concluded that the orientation and burrow architecture of *Ophiomorpha nodosa* can be used to distinguish deposits of relatively low energy regimes from those of higher energy environments, particularly those with variable rates of sedimentation (Frey et al., 1978; Anderson and Droser, 1998). However, these studies also underscore *O. nodosa*'s architectural variability. The predominant burrow architecture of *O. nodosa* in the Miocene tidal-channel margin deposits could not be determined with confidence. The observed 3:1 ratio of tunnels to

shafts suggests a three-dimensional architecture with more horizontal components than vertical components (e.g. mazes or boxworks). However, tunnels may be over-represented because they are more likely than shafts to be intersected by the vertical plane of the outcrop. Only one specimen displayed branching linking it to a boxwork structure, and, although groups of vertically closely spaced tunnels were common, they were not clearly organized into maze structures.

Studies of the burrow architecture and behavior of modern thalassinidean shrimp have led to classifications that link architecture to feeding mode (e.g. Griffis and Suchanek, 1991; see summary in Bromley, 1996; Griffis and Chavez, 1988 for alternative views). The ability to infer feeding behavior from burrow architecture would be a boon for paleoecologic interpretations. However, the lack of a consistently identifiable, recurring three-dimensional structure in *Ophiomorpha nodosa* within the Miocene channel-margin deposits suggests that within-habitat variability may preclude reliable linkage between architecture of the burrow system and feeding habit. This variability may also reflect behavioral and trophic plasticity, as has been documented in recent studies of modern thalassinideans (e.g. Nickell and

Table 3

Summary of variations in *Ophiomorpha nodosa* and related trace fossils reported in the literature and the behavioral or environmental interpretations. These variations were not observed in this study

Observation	Behavioral or environmental interpretation	Source
Well-pelleted tunnel roofs, smooth floors	Response to greater need for reinforcement of roof wall than rest of burrow	Frey et al., 1978
Variation in thickness and pelletization of wall corresponding to depth beneath sediment–water interface (SWI) and to inferred original sediment cohesiveness (e.g. in heterolithic sequence, sands originally less cohesive than mud)	Shrimp produced thicker-walled and more highly pelleted burrows in less cohesive versus more cohesive sediments	Ager and Wallace, 1970; Kennedy and Sellwood, 1970; Bromley and Frey, 1974; Kern and Warne, 1974
Older parts of burrows pelleted; newer portions are thinner walled and may lack pellets	Producer of this burrow form was a deposit feeder that used pelleted older section of burrow as dwelling; other portion of burrow system was used for deposit feeding	Asgaard and Bromley, 1974
Apertural necks branch off from shaft at different levels	Shrimp re-establishes contact with SWI after erosional or depositional events	Frey et al., 1978
Domination by mazes or boxworks (not shafts) in sands overlying impenetrable layers	Adjustment of depth of burrowing and burrow architecture where deep burrowing is blocked	Frey et al., 1978; Fürsich, 1974
<i>Gyrolithes</i> present in association with <i>Ophiomorpha</i>	Different ichnogenera reflect behavioral change of single type of tracemaker in response to change from sand to interbedded sand and mud	Hester and Pryor, 1972
<i>Teichichnus</i> present in association with <i>Ophiomorpha</i>	Single producer for both trace fossils; <i>Teichichnus</i> produced in response to adjustment of burrow relative to SWI	Hester and Pryor, 1972
Shafts dominate in high-energy environments, mazes and boxworks in lower-energy environments	Burrows are deeper in intertidal zones. Higher sedimentation rates promote formation of shafts versus tunnels	Frey et al., 1978; Anderson and Droser, 1998

Atkinson, 1995; Nickell et al., 1998). Extensive behavioral plasticity has led some to question the validity of attempts to classify modern thalassinidean burrow systems (Bishop and Bishop, 1992; Rowden and Jones, 1995). Increasing understanding of thalassinidean behavior (Stamhuis et al., 1996), of the variety of food resources used by thalassinideans (Murphy and Kremer, 1992; Schlacher and Wooldridge, 1996; Boon et al., 1997; Stamhuis et al., 1998), and of the mechanism for mucous secretion for burrow construction (Dworschak, 1998) support the suggestion that future efforts to classify burrows should focus on burrow wall characteristics or individual components of the burrow system. These reflect functioning of the animals more faithfully than does architecture of the burrow system (Swinbanks and Luternauer, 1987; Nickell and Atkinson, 1995). Wall characteristics also have been found to be less variable than burrow architecture in fossil burrows (*O. nodosa*; Frey et al.,

1978). However, the wide variation in burrow-margin characteristics documented herein demonstrate plasticity in wall-building behavior, although it may be less than variation in the behavior controlling burrow-system architecture.

4. Behavioral response of *Neotrypaea californiensis* to environmental perturbation

4.1. Approach

Studies of the burrowing of modern thalassinidean shrimp have established that the burrow systems vary widely, even within a single species (Rowden and Jones, 1995). Experiments were conducted to document how modern burrowing shrimp would respond to environmental change and how this change would be reflected in burrow morphology. The plan was to

bury shells in layers within sandflats densely populated by *Neotrypaea californiensis* (formerly *Callinassa californiensis*; see Manning and Felder, 1991). Sandflats between the upper margins of the tidal channel and the lower marsh of Mugu Lagoon, California (located at Point Mugu Naval Air Station) have had mean densities of shrimp of 169 m^{-2} and mean densities of burrow openings of 385 m^{-2} (Miller, 1977, 1984; Miller and Myrick, 1992). However, in response to the US Navy's request to reduce negative environmental impact, layers of glass plates (2 cm \times 2 cm \times 1 mm) were substituted for layers of natural shells. Layers of glass plates were implanted 10–15 cm beneath the sediment surface. After 12 months many burrow openings had appeared at the sediment surface above the glass plates, implying that *N. californiensis* had burrowed through or around the layers. At that time, to determine whether the shrimp could burrow around an impenetrable layer, a 0.25 m² piece of screen-door netting was buried 10–15 cm below the sediment surface. After 13 months from the initiation of the experiment, the plots were revisited and the number of burrow openings at the surface counted. The quantitative data in this experiment involve the re-establishment of burrow openings (Miller et al., 1990; Miller, 1991) and are not discussed here. To determine whether the shrimp were living above the layers of glass plates or circumvented or penetrated the glass layers, epoxy resin casts were made of seven burrow systems, including two in control plots with no glass layers. A resin cast was also made of a burrow system above the screen netting. As in other studies of the morphology of thalassinidean burrow system morphology (e.g. Griffis and Chavez, 1988), casting of a sufficiently large number of burrows for a quantitative sample was precluded by the potentially large negative environmental impact on the shrimp population and sandflat ecosystem.

4.2. Results

Comparison of resin casts of burrows made in control plots (no glass plates), in those with glass plates, and in the screen-netting plot demonstrated the behavioral flexibility of *Neotrypaea californiensis*. *N. californiensis* typically produces deep Y-shaped burrows (e.g. Griffis and Chavez, 1988), and this is the morphology of the burrows in the control

plots (Fig. 7A). In contrast, the five burrow systems casted in plots with layers of glass plates have densely packed burrows above the glass layers (Fig. 7B). In each cast, a few burrows extend below the layers of glass plates (Fig. 7B), indicating that the shrimp could penetrate the layer of glass. However, shrimp activity, as reflected by burrow density, was concentrated above the glass plates, and no burrows extended around the layer of glass plates. The resin cast of a burrow system in the screen-netting plot showed that the shrimp encountered the screen netting as it moved downward, burrowed to the margin of the netting, and constructed a burrow extending downward from the edge of the netting. This indicates that, when confronted with an impenetrable layer, as opposed to potentially movable glass plates, the shrimp circumvented the obstacle.

4.3. Discussion

Neotrypaea californiensis alters its behavior to deal with environmental perturbations, at least those presenting barriers to its preferred deep-burrowing habit. Previous work has documented that *Callichirus major* (formerly *Callinassa major*) restricts its burrow to shallow depths (<30 cm) in areas where a thin veneer of sand overlies consolidated muds or shell layers that are difficult to penetrate; in otherwise suitable habitats, *Callichirus major* is absent from some areas that are underlain by relict muds (Lunz, 1937, in Frey et al., 1978). Restriction to a thin zone just beneath the sediment-water interface presumably increases the chance of predation, in the case of *Neotrypaea californiensis*, by shorebirds and fish (M.F.M., personal observation; Posey, 1986).

Resin casts of burrows in experimental plots with layers of glass plates indicate that *N. californiensis* actively investigated the layers to find a means to penetrate the barriers and establish burrows at the preferred depth. The resin cast in the screen-netting plot demonstrated that the shrimp located the edge and burrowed downward. When confronted with glass plates, the shrimp either found a sufficiently large gap to burrow through or created one by moving a glass plate laterally. Altering depth of burrowing and burrow morphology reflects behavioral plasticity. Finding a way around the barrier indicates more sophisticated behavioral flexibility, allowing

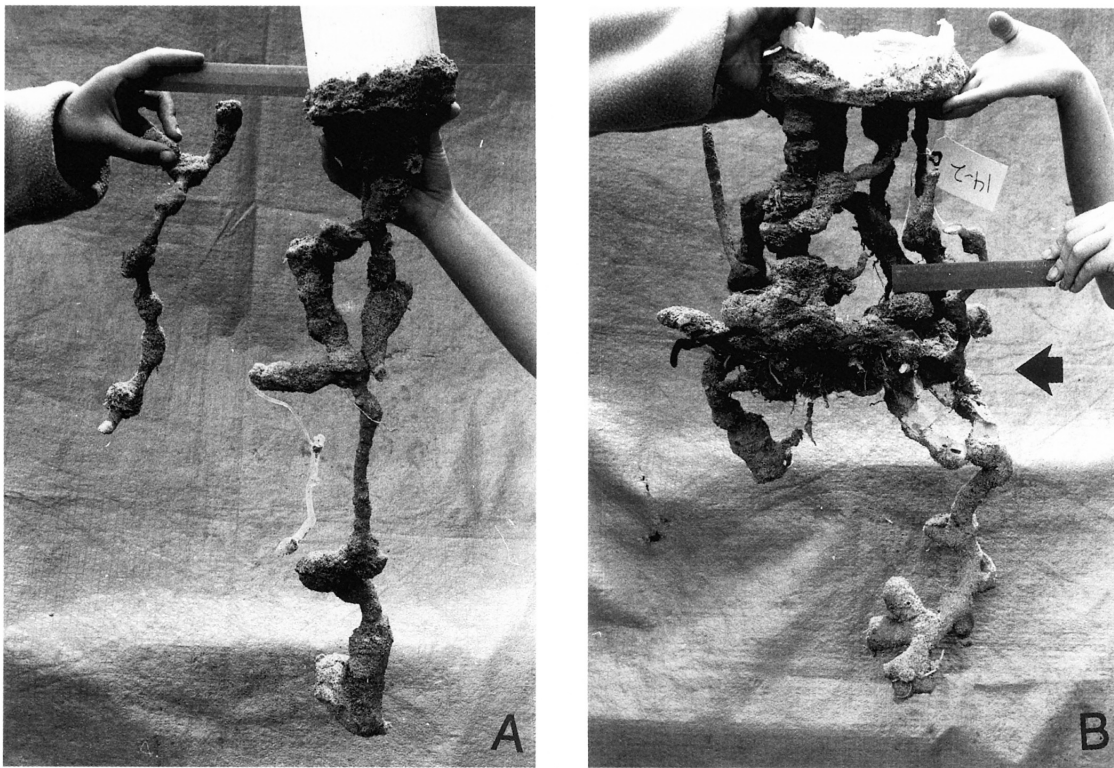


Fig. 7. Epoxy resin casts of modern burrows of *Neotrypaea californiensis* (formerly *Callinassa californiensis*) from Mugu Lagoon, California. (A) Predominantly vertical burrow systems formed in the absence of a barrier created by a layer of glass plates. (B) Burrow system developed in the presence of a solid layer of glass plates. Arrow points to level of that layer. Note the abundance of burrows above the layer. A few shrimp actually moved the glass plates to penetrate the barrier.

N. californiensis to overcome the barrier rather than simply to adapt to it.

5. Behavioral response of producers of Miocene and Pleistocene thalassinidean burrows to bioclastic obstacles

5.1. Geologic setting

The response of thalassinidean burrowers to within-sediment obstacles was evaluated by assessing the abundance of burrows and the behavior of the producers in shell accumulations (Miocene, Maryland) and in coral reef rubble (Pleistocene, Bahamas) (Table 1). In these deposits, Ophiomorpha is the most common thalassinidean-produced trace

fossil. However, in the Miocene of Maryland, other trace fossils produced by thalassinideans, including *Thalassinoides* (without pelleted burrow walls) and *Gyrolithes* (with spiral form and without pelleted walls) are present, although less abundant.

In the Upper Miocene of Maryland, we focused on two shell beds: the Boston Cliffs shell bed in the Choptank Formation and an unnamed, thin shell accumulation in the Little Cove Point Member of the St. Mary's Formation, here called the "*Turritella*" shell bed (Kidwell, 1989). The Boston Cliffs is a thick (up to 3.6 m), laterally extensive shell-supported shell accumulation (Kidwell, 1989). Like other thick shell beds of the Miocene succession in Maryland, the Boston Cliffs is interpreted as a condensed transgressive lag deposit that formed on an open marine shelf

(Kidwell, 1989). The complex internal stratigraphy, dense packing of shells, faunal composition, and other characteristics indicate that the shell layer records slow accumulation with repeated episodes of erosion, winnowing, and reworking. The lower part of the Boston Cliffs probably was subjected to “dynamic bypassing” (Kidwell and Aigner, 1985; Kidwell, 1989) characterized by alternation of periods when sand blanketed the shells and periods of winnowing and reworking. The periods of sand deposition probably provided colonization windows for infaunal animals (Pollard et al., 1993), including the thalassinidean producers of *Ophiomorpha nodosa* and *Thalassinoides*. Shell packing in the Boston Cliffs is dense-loose in the terminology of Kidwell and Holland (1991); there is a significant amount of sand matrix between the shells. Shells are poorly sorted; they range from 4 mm to over 250 mm in longest dimension.

In contrast, the “*Turritella*” shell bed in the St. Mary’s Formation is thin (10–25 cm thick) and composed primarily of turritellid gastropod shells. These shells are small, mostly 1–2 cm in longest dimension, and well sorted. They exhibit the “dense” packing of Kidwell and Holland (1991), with very little sand matrix between the shells. The internal stratigraphy of the “*Turritella*” bed is simple; it reflects a limited number of depositional and winnowing events rather than the complex history of the thick Boston Cliffs shell bed.

Ophiomorpha also is a widespread and common trace fossil constituent of shallow subtidal, shelly to reefal Pleistocene calcarenites throughout the Bahamas (Curran and White, 1991; Curran, 1994). For this study, we focused on the occurrence of *Ophiomorpha* in facies of the late Pleistocene coral reefs at Cockburn Town on San Salvador Island and at Devil’s Point on Great Inagua Island. A significant point here is that the *Ophiomorpha* tracemaker organisms were not excluded from or deterred by substrates consisting of large chunks of coral rubble. Indeed, some of the most robust *Ophiomorpha* burrow systems that either of us have ever seen occur in the coral rubblestone facies of the Devil’s Point coral reef on Great Inagua Island (White and Curran, 1995; Wilson et al., 1998).

5.2. Approach

For the Maryland Miocene study, the type of packing (Kidwell and Holland, 1991), and size and sorting of the shells was evaluated at 1 m intervals ($n = 30$) along the vertical exposure of the St. Mary’s Formation that contained the “*Turritella*” bed. Ichnofabric indices (Droser and Bottjer, 1986) of the superjacent and subjacent layers were noted, and the number of burrows present in a 0.0625 m² vertical section of the shell bed counted. Fallen blocks of the Boston Cliffs shell bed were examined in vertical and horizontal (bedding plane) sections. Type of packing was evaluated on vertical surfaces and observations (0.0625 m²; $n = 418$) of shell size and sorting and number of thalassinidean burrows were made on bedding planes. In the Bahamian Pleistocene reefal deposits, the occurrences of *Ophiomorpha* in the various facies of the reef complex were carefully noted, described, and photographed.

5.3. Results

Thalassinidean-produced burrows, including *Ophiomorpha* and *Thalassinoides*, were present but not abundant within the Boston Cliffs shell bed. In the 418 bedding-plane observations, 42 thalassinidean burrows were noted. The burrows wind around large shell fragments; the thalassinidean producers were actively avoiding the largest shell particles (Fig. 8).

In contrast, the thinner “*Turritella*” bed contained no *Ophiomorpha* or *Thalassinoides*. *Gyrolithes*, the spiraled thalassinidean-produced trace (Frey et al., 1978; Dworschak and Rodrigues, 1997), is common both above and below the “*Turritella*” bed (Christiansen and Curran, 1995).

The lithified late Pleistocene reef rubble of Bahamian fossil coral reefs commonly contains *Ophiomorpha*, indicating that the tracemakers could successfully cope with large pieces of coral while forming robust and extensive burrow systems within the rubble substrate. One of the best examples is within the rubblestone facies of the upper part of the Devil’s Point coral reef on Great Inagua (Fig. 9; Wilson et al., 1998). This setting also provides a clear example of the behavioral response of the *Ophiomorpha* producers to an impenetrable surface, in this case a lithified erosion surface that formed within the reef sequence prior to the deposition



Fig. 8. White arrow points to a large burrow made by a thalassinidean that moved around shells within meters-thick shell accumulation. A complex history of shell accumulation (Kidwell, 1989) combined with relatively loose packing of shells allowed animal to colonize and move through the shell-rich layer. Boston Cliffs shell bed, Miocene of Maryland.

of overlying rubblestone beds. When the *Ophiomorpha* producers encountered the lithified surface, they immediately began to tunnel along this surface, forming complex maze patterns (Fig. 10).

5.4. Discussion

Like their modern counterparts, the thalassinidean producers of Miocene and Pleistocene *Ophiomorpha*



Fig. 9. Robust *Ophiomorpha* specimens in Pleistocene coral rubblestone, Devil's Point reef, Great Inagua, Bahamas. White arrows point to fragments of acroporid corals; black arrows point to segments of *Ophiomorpha* burrows. Note that the burrow at left is anchored to the chunk of coral.



Fig. 10. *Ophiomorpha* maze formed when the tracemakers encountered an impenetrable lithified surface within the Pleistocene coral reef sequence. Devil's Point reef, Great Inagua, Bahamas.

were capable of adjusting their behavior to circumvent barriers. Just as the behavioral flexibility of *Neotrypaea californiensis* went beyond altering the depth of burrowing to going around or through the barrier, so too the Miocene and Pleistocene *Ophiomorpha* producers made opportunistic choices when confronted with immovable objects.

Episodes of low shell input and sand accumulation provided opportunities for burrowers, including thalassinideans, to colonize the Boston Cliffs shell bed as it was accumulating. The combination of poorly sorted shells, large shell size, and dense/loose (versus dense) packing allowed the burrowers to move between shells within the shell bed. In contrast, the thinner "*Turritella*" bed presented an impenetrable barrier to thalassinidean burrowers. They apparently could not deal with the dense packing of uniformly sized shells and the paucity of interstitial sand. Rapid deposition of the shell bed without periods of winnowing and sand deposition prohibited colonization by thalassinidean burrowers during shell-bed accumulation, which would have facilitated "loosening" of the shells by burrowing activity.

The Pleistocene coral-reef rubble consists of abundant and large chunks of coral with a variable amount of shelly, carbonate sand matrix. Although this mixture presented a complex substrate that commonly was sand-poor, the thalassinidean producers of *Ophiomorpha* were capable of moving around coral chunks and maximizing use of the available ecospace. The impressive aspect of this reefal occurrence is how common the large-diameter (typically up to 5 cm or more in outside diameter) and very thick-walled burrows of *Ophiomorpha* are in this setting. In addition, considerable behavioral plasticity is in evidence. Given that matrix material within the coral rubble layers commonly is minimal, the vertical to oblique segments of the burrow systems frequently are anchored to the surfaces of the coral chunks, providing direct support for these large burrow systems.

In addition, barriers in the form of large and flat coral chunks usually elicited tunneling behavior from the *Ophiomorpha* producers. As described earlier (see also Wilson et al., 1998), the ultimate transition to tunneling behavior occurred when the burrowers formed extensive maze systems over the lithified

erosion surface within the reefal sequence in the Devil's Point reef on Great Inagua.

The junior author has had much experience with modern coral reefs in the Bahamas and wider Caribbean. In conducting taphonomic studies of modern coral reef rubble using scuba gear, many likely thalassinidean burrow holes entering the rubble substrate have been observed. However, sediment mounds and fecal pellet accumulations typical of the burrowing activities of thalassinideans normally are not present owing to the generally high-energy settings of these substrates and the redistribution of surface sediment by wave action. Interestingly, it is the fossil occurrences that have revealed the true extent of thalassinidean activity and burrowing within the coral-reef setting.

6. Conclusions

Although the role of physical environmental parameters in controlling optimal burrowing organism behavior and, thus, the morphology of the traces they produce has been well documented for marine settings, it is not clear how closely behavior and trace morphology are linked to environmental conditions on a smaller scale. In this study, questions designed to elucidate the effects of subtle environmental change on behavior and trace morphology, to evaluate the amount of behavioral variation in the absence of environmental change, and to assess the behavioral flexibility of modern and ancient thalassinidean shrimp yielded the following information.

1. Miocene producers of *Ophiomorpha nodosa* preferred the margins of tidal channels to the channel axis. As reflected in trace abundance and morphology, the tracemakers responded to the higher energy channel-axis conditions by avoiding this environment rather than by altering behavior.
2. Traces produced within the channel-margin facies vary widely, in wall structure, burrow fill, and burrow-system architecture. The tracemakers were inconsistent in pelleting their burrow walls, and they made frequent forays outside of their pelleted burrows where they disrupted the sediment without constructing burrows. No common burrow architectural style was identifiable within

the apparently homogeneous channel-margin facies.

3. When their habitat is altered by the introduction of a nearly impenetrable layer within the substrate, modern thalassinidean shrimp respond by modifying the burrow architecture to create more burrows at shallow depths beneath the sediment surface, or by finding a way around or through the barrier.
4. Miocene and Pleistocene thalassinideans burrowed around shells and coral rubble, unless the skeletal debris was well-sorted and densely packed, resulting in an impenetrable barrier.

Although constructing a neatly pelleted burrow (i.e. the classic form of the trace fossil *Ophiomorpha nodosa*) requires complex, rigid behavior, thalassinideans, including makers of *O. nodosa*, are and were behaviorally flexible, producing variable burrows. Absence of significant morphological difference in *O. nodosa* produced in two different environmental regimes (channel margin versus channel axis, Miocene of Delaware), in concert with wide within-facies variation in *Ophiomorpha nodosa*, indicate that differing physical parameters do not necessarily trigger changes in behavior that are reflected in trace fossil morphology. The ability of modern, Miocene, and Pleistocene thalassinideans to cope with obstacles within the substrate reflects remarkable behavioral opportunism. Thalassinidean behavior is complex, variable, and not necessarily intimately linked to environmental conditions. Given the possibility that thalassinidean behavior may mirror that of other infaunal, tracemaking animals, care should be taken in attributing morphological variation in traces to variations in environmental regime.

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